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ONCHIDIUM AND THE QUESTION OF ADAPTIVE COLORATION[1]

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I. As the result of his extensive study of the phenomena of coloration in the tropical reef-fishes, Longley (1917) comes to the conclusion that the colors of these animals are "correlated with their habits in such a way that their conspicuousness is thereby reduced. There is no correlation of bright colors with special modes of defence, and no evidence that bright-colored types enjoy immunity greater than that of their fellows." The general tendency of this, the most recent, and in many ways the most thorough, observational study of the question of adaptation in animal coloration that has yet appeared, favors adherence to the view that as a whole the coloration of animals is of a concealing, hence adaptively protective kind. There are instances among invertebrates which seem fundamentally inconsistent with this interpretation, because the organisms in question are not colored like their habitual background and because they are for this, and for other independent reasons not inconspicuous. It is also a fact that in specific instances of this sort special repugnatorial systems are frequently encountered. Because of its importance for the theory of adaptation, this matter is deserving of careful scrutiny. The natural history of the littoral pulmonate *Onchidium floridanum* Dall affords a case in point.

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[1] Contributions from the Bermuda Biological Station for Research and from the Anatomical Laboratory of the Northwestern University Medical School.

In his notes on the fauna of Bermuda, Heilprin (1889, p. 187) described as new the form "Onchidium (Onchidiella) trans-Atlanticum," saying of its pigmentation: "smoke color or dark olive," in dorsal view. Some years later Pilsbry (1900, p. 503), reporting on Verrill's collections at Bermuda, listed this species under the designation by which it is now known, *Onchidium floridanum* Dall, adding, "Its dark olive green color agrees so well with the stains on the rocks that it is very inconspicuous. —(A.E.V.)"

It is possible, though not certain, from these brief descriptions, that Heilprin and Verrill had respectively collected representatives of the two differently colored types of *Onchidium* which occur at Bermuda. No constant morphological differences have been detected upon which to base a separation of these types, one of which is in nature blue-black in general aspect, the other characteristically of a light ("smoky") olivaceous hue. Some intermediate shades do occur, but in the field a rather sharp separation of the two groups is always possible. The very dark form is much the more numerous. So far as pigmentation is concerned, it is probable that the blue-black types contain merely a heavier deposit of a subepidermal pigment, which is chemically alike in both kinds of Onchidia. Nevertheless, we are inclined to believe that the difference in pigmentation may be representative of a real genetic difference between the two types, for reasons which may briefly be stated as follows: The two modes of colorization are in many places exemplified side by side; young and adults of maximal size are found belonging to either group; the occurrence of the pale form is independent of the seasons, and is found year after year in the same spots; in other places, where blue-black individuals may be very numerous, no lightly pigmented individuals have ever been encountered. Therefore we are probably dealing, not with a temporary fluctuation in color, determined by some metabolic cycle, but with constitutionally diverse races of *Onchidium;*

whether they be "species" or not is immaterial. A similar phenomenon seems to occur in other genera of this family, for v. Wissel (1898) notes that Plate (cf. Plate, 1893, 1894) collected two differently colored forms of *Onchidiella coquimbensis* Plate; in this instance the color difference between the two types, found in nature under the same stones, was not so pronounced as we find it in *O. floridanum*. In an *Onchidiella* which is very abundant at Bermuda one of us has observed a corresponding sort of color difference. The variation in question cannot be in any way a sexual one, for reasons already given and because the animals are hermaphroditic.

II. *Onchidium floridanum* lives between tide levels. It is never seen when the intertidal shore-zone is covered by the sea; during this period it inhabits deep crevices and cavities within the eroded rock. A dozen or more Onchidia live together in this way. Their "nest" opens to the exterior by means of a small opening, usually further obstructed by the growth of *Modiolus*, which is almost invariably quite inconspicuous, although the densely packed small black "mussels" within and around the entrance itself may form a very definite patch standing out clearly amid the olive-brown algæ covering the surface of the rock. When the tide falls so far as to have left the level of the *Onchidium* nest about an hour before, the occupants of that nest emerge, successively and in a steady stream, wander some little distance over the rock, feed, and then, before the tide has risen again, the members of each group synchronously begin to creep back to the respective nests from which they originated. The remarkable character of this "homing" behavior we have separately studied with considerable care, and have discussed in another place (Arey and Crozier, 1918). Here we would emphasize simply the fact that *O. floridanum* appears in the open, on the intertidal rocks, only during the period of low water.[2]

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[2] The experimental observations from which some of these statements are derived will be found described in a report, by Arey and Crozier, on the general behavior of *Onchidium*, now in course of preparation.

The nature of the background provided on this rock surface is by no means constant in different localities. Commonly, as in the case of rocks in sheltered places, completely submerged at high water, or on lee-shores generally, the limestone is covered by a feltwork of matted Enteromorpha and associated plants, sun-bleached to an olivaceous yellow tint. This is the usual condition within the sounds (Great Sound, Castle Harbor), and along the shores of bays protected from the surf. In places not so sheltered the rock may be colored by minute green algæ, or by the growth of calcareous green or reddish algæ, with which, as in the former case, many serpulas are intermingled; barnacles (*Tetraclita porosa*) also sometimes extend into the *Onchidium* zone, but the prevailing hue, and the color of any particular spot of small area, is largely determined by algæ.

Onchidium also occurs, though more sparingly, on surfaces of a still different type. In some places the layer of red earth (clay) underlying superficial æolian limestone is exposed at the water's edge, usually in a small cove containing loose rocks left bare by the tide. This earth provides a muddy layer of reddish brown, over which Onchidia are occasionally found to be creeping. From such tiny coves the direct rays of the sun are largely excluded, so that the in-shore surfaces of the stones are overgrown by algæ, green or red-brown, unbleached; on these surfaces also *Onchidium* may be found.

The zone inhabited by *Onchidium* is also that in which great numbers of the common *Modiolus* occur. These mussels, as already stated, almost invariably line the approaches to the *Onchidium* nest, and grow within the entering passageway itself. Except where the mussels have settled thickly in more or less horizontal fissures between the wind-formed strata of the limestone, they occur conspicuously in little groups, frequently not more than 3–4 cm. in diameter, occupying every slight depression in the surface; this is usually the case in situations where *Onchidium* abounds. A typical instance is that of a low-lying islet such as "Little Agar's," in Great Sound. The leeward (eastern) side of this island, well protected by the mass of the larger Agar's Island, exposes at low water a considerable extent of almost horizontal rock-surfaces, whereon occur sparingly clumps of *Modiolus,* which are, however, much more abundant around the vertical edges of these slabs. Within the clumps of *Modiolus* lie many *Onchidium* nests, from which the mollusks at appropriate times creep out and wander over the flat, yellowish, sunlit beach-rock. It is in situations of this general type that *Onchidium* is most abundant; in less freely illuminated places it occurs more sparingly.

It is a remarkable fact that, in addition to frequenting characteristically, though not exclusively, habitats which during most of the day receive the direct rays of the sun, *Onchidium* comes out into the open only during daylight hours, and never (in our experience) at night;[3] the circumstance which makes this condition particularly curious is that O. *floridanum is at all times negatively phototropic,* and in a very precise manner, when tested apart from its usual environment. No more striking instance is known to us of apparent contradiction between the findings of analytical experimentation regarding the behavior of an animal and the actual life of the same creature, for the snails when on the intertidal rocks move toward or away from the horizontal rays of the sun with perfect indifference. The cloudiness or brightness of the day, however, has but an unimportant influence, if any, on the numbers of Onchidia which appear upon the rocks.

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[3] That the wandering of *Onchidium* into the open is determined by immediate physical circumstances in the environment is shown by two facts: No rhythmic periods of migration persist when the snails are removed to the laboratory; on days when strong winds and accompanying ocean currents prevent the escape of the tidal water from the partially enclosed Great Sound, so that there is no occurrence of "low water," the Onchidia remain within their nests. *O. floridanum* can remain below water for 6–7 days without much impairment; a small amount of air is sometimes trapped within the rock cavities which they utilize as nests and this may in some cases help during prolonged submersion.

III. The coloration of an *Onchidium* is the result of its intensity of pigmentation, the texture of its mantle, and the activity of its mantle glands. An adult measures, on the average, 17 mm. long by 12 mm. broad by 6 mm. high when resting undisturbed, being then oval in outline; but it becomes more elongated during creeping, measuring then about 24 by 8 mm., and also less strongly arched, being about 4 mm. high. When first observed creeping out of its nest for an ''airing,'' it usually happens that the *Onchidium* bears upon its dorsal surface a thin pellicle of slime completely investing the mantle. This slime-layer is tough, somewhat thickened about the periphery, and can be peeled off intact. Frequently it is so removed, mechanically, during the snail's efforts to creep out of its nest, for the passage-way is commonly so obstructed by the growth of *Modiolus* that the Onchidia must slowly insinuate themselves through slit-like apertures not more than 2 mm. wide. Occasionally Onchidia are seen creeping about with their slime-coat but partially removed.

The slime-pellicle is encrusted with the muddy fecal matter which the Onchidia deposit. This calcareous mud is swallowed when feeding on the algæ over which they creep in the open; it represents the ordinary silt of the shore-line, and may in part be chemically abstracted from the thin layer of sea-water covering the algæ as the tide recedes, owing to photosynthetic removal of CO_2, especially as accelerated by increasing temperature and by isolation as the sea-weeds become more exposed.

When the slime-coat is removed, an ordinary *O. floridanum* seems at first sight jet black; the mantle is wet and shiny; closer examination shows that the color is really a very dark and smoky olive. The mantle-glands continue their slime secretion, however, and by the action of wind and sun the surface of the mollusk quickly assumes a dry blue-black aspect, its numerous papillæ glistening in the light; the appearance of the mantle, with a slight ''bloom'' on it, then resembles that of the tiny thysanurans so common on the beach sands and also on the rocks where *Onchidium* lives.

Typical Onchidia of the lighter colored variety appear at all times light olive or greenish yellow. The coloration is not "solid," for the dark-hued internal organs usually show through as one or more dull blackish patches. The edge of the mantle is quite pale.

It has not been possible to convert one variety into the other by laboratory experimentation. The dark Onchidia are still dark after six weeks complete starvation.

Onchidia of either type are found, frequently side by side, in all the varieties of habitat which we have described. To mention some specific localities, we may list the following: Bailey's Bay; Flatt's Inlet; the east side of the channel entrance to Hungry Bay, at its inner end; an island at the entrance to Fairyland Creek; a small cove on Burgess Point. These situations are widely separated, and cover the different sorts of backgrounds to which allusion has been made.

Not only in a general way, merely, but also in any given place where they occur, the lightly pigmented Onchidia fail to indicate by any peculiarity of behavior that they differ essentially from the dark ones. That they are easily overlooked is quite true; they are homochromically colored in practically all the instances that have been observed. But it should be noted that in one such place the homochromically colored individuals were found in the proportion of but one to nearly 190 of the dark black ones. This was on a greenish rock surface of northern exposure where a color-changing form like the isopod Ligia was pale-greenish, like the pale Onchidia. In other places more or less isolated colonies of fifty or more pale specimens were encountered. In some cases the coloration was decidedly greenish, rather than olivaceous yellow.

IV. The numerous dorsal papillæ of *Onchidium* were said by Semper (1877, 1881) to indicate the location of mantle-eyes; since, however, no sensory nerve-terminals were at that time demonstrated within the "eyes," some writers followed Joyeux-Laffuie (1882) in the opinion that the "dorsal eyes" of Semper were in reality mantle glands, corresponding to those undoubted glands found in the related genus *Oncidiella* (cf. v. Wissel, 1898). The more complete analysis of the histology of the mantle in *Onchidium* by Stantschinsky (1908), nevertheless, proved that the "dorsal eyes" do possess nervous structures appropriate for photoreception, the retinulæ being, in addition, of the inverted ("vertebrate") type. *O. floridanum* possesses, however, repugnatorial mantle glands as well, which are not associated with the dorsal papillæ, these last being relatively minute.

The glands are comparatively large, but are easily overlooked in an undisturbed *Onchidium*. The periphery of the mantle has a frilled appearance, numerous tiny projecting papillæ giving it a serrated outline. If the animal be disturbed, the tissues surrounding each of the glands become erected, and 14 stout conical papillæ, 7 on either side and each with a terminal pore, become evident.

If the animal is suddenly removed from the rock by grasping its dorsum, the glands all become turgid, point upward and inward, and quickly discharge by the contraction of their muscular investments. The secretion is a viscid fluid, milk-white, non-miscible with sea-water, and decidedly acid in reaction. Discharge is more easily elicited in air than when the animal is submerged. Under water the secretion is expelled in long threads, but in air the stream as it leaves the gland breaks up into a fine spray, which may be shot to a distance of 12–15 cm. With vigorous stimulation, as when the back of the *Onchidium* is pinched with forceps, the discharge appears from every gland as a stream about 0.2 mm. in diameter, which is often too stout to form fine droplets. In nature, however, the initial repugnatorial discharge is less copious; it then takes the form of a fine spray, almost invisible, which may be thrown for as much as 15 cm., or about ten times the length of the *Onchidium*.

As discharged, the secretion is found to contain at least three elements visible under the microscope: a clear fluid, apparently water; clear droplets of oily appearance; and a finely granular material. The relative proportions of these three elements vary in different glands. An individual tested in the field, without previous disturbance, usually secretes a densely granular mass containing a fair proportion of globules; in the activation, a good deal of the secretion usually adheres to, or falls back upon, the mantle of the snail itself—the dryness of the mantle, and the fact that in nature violent discharges of secretion seem seldom to be invoked are important for the freedom of the mantle from being itself sprayed. On the other hand, the fluids ejected from one or more glands of starved Onchidia are almost always clear and watery, sometimes with no trace of the granular or droplet constituents. Variation in the composition of the corresponding glands of *Oncidiella* was recognized by v. Wissel (1898), who also discovered the secretion droplets (globules) which previous workers had overlooked.

When the secretion adheres to the mantle of an *Onchidium,* it can be seen that considerable stimulation of the skin is thus produced. The secretion is quite acid to litmus and to a number of other indicators. The acid is found in the dense granular material, and does not occur, save in relatively slight amount, when this material is absent. The white masses may be caught on a clean slide and studied under the microscope. The granular material is insoluble in 90 per cent. alcohol, or in water. If indicators are added to a drop of the secretion under a coverslip, it can be seen that the acid slowly diffuses out into the water from the granular mass.

The white substance, if received on the tongue, is found to sting with considerable persistence, like wild mustard. It does not taste sour. Plate, testing the secretion of the mantle-glands of an *Oncidiella,* found "dass das Secret dieser Drüsen auf der Zunge ein deutlich wahrnehmbares

Brennen hervorruft" (according to v. Wissel, 1898, p. 597).

Stimuli initiated in several different ways may serve to elicit discharge of the repugnatorial glands, as: stroking the mantle with a blunt point; pinching it with forceps; applying solutions (5/8 M) of NaCl or (less effectively) LiCl, or of methyl or ethyl alcohol (5 M). Touching or pinching the *periphery* of the mantle itself does not lead to discharge, but on the contrary leads to localized retractive puckering; when a gland is erected, preparatory to discharge, stimulation of that gland causes it to collapse, or "wilt," a process similar to that following normal discharge. If the dorsum be scratched until erection of the glands occurs, and then NaCl solution be applied to one of them, it is found, as also with mild faradization, that two or even three successive discharges are possible; but the later out-pourings of secretion are very meager as compared with the first explosive ejection. About twenty-four hours is required for the regeneration of a new supply of repugnatorial substance.

Before the glands discharge, the edge of the mantle curls upward, forming around the *Onchidium* an encircling saucer-edge bearing the now prominent glands; thus, depending upon the intensity of excitation, the glands come to point more and more dorsal, and in this position release their contents. Not only so, but the individual gland papillæ are themselves further directed in a general way toward the irritated spot, so that if a slip of glass be held horizontally 1 or 2 cm. above an *Onchidium* the back of which is at one point subjected to mild faradic excitation, the contents of all the discharging glands are found to impinge upon very nearly the same point; sometimes all the discharges converge to an area of less than 3 × 3 mm., immediately above the spot irritated. The gland or glands nearest the site of stimulation are the first discharged, and the implication of more distant ones depends on the degree of stimulation.

Semper (1881, p. 372 *et seq.*) considered that the dorsal eyes of *Onchidium* were employed in sensing the approach of animals which might attack it. He had in mind the attacks of the Philippine *Periopthalmus,* a blenny which, leaping along the intertidal beach-zone on its ventral fins, feeds upon *Onchidium* and on arthropods. Semper thought that the eyes of the Onchidia rendered them sensitive to the shadow of an approaching fish, whereupon a fluid spray was discharged from the skin glands, driving off the fish. Whether Semper regarded the secretion as repugnant to the fish in a chemical way, or whether it was to act in a mechanical fashion merely, is not altogether clear. Semper endeavored to make out a correlation, illustrative of evolutionary principles, between the geographical distribution, on the one hand, of the species of Onchidia possessing dorsal eyes, and, on the other, of the genus *Periopthalmus.*

There are at Bermuda no *Periopthalmus,* nor any other fishes of similar habits. *Onchidium floridanum* is, however, quite reactive to shading. The dorsal surface of the mantle is the part sensitive to decrease of light intensity. In a moving *Onchidium* the ensuing reaction involves a momentary cessation of creeping, retraction of the tentacles, and a depression of the periphery of the mantle to the surface of the rock. The tentacles themselves, which in air are much further protruded than when under water, are not photosensitive. An *Onchidium* shaded when not creeping, but at rest or feeding, exhibits the same type of response, but the mantle is more decidedly humped. But, in our experience at least, no discharge of the repugnatorial glands is induced by shading. This does not mean that Semper's observations were not correct. In *O. floridanum* the type of excitation which is preeminently and characteristically effective for gland discharge is of a mechanical nature, namely, a rubbing or pinching of the apex of the dorsum or a dislodging thrust upon the ventral surface of the girdle. Although when tested by faradic excitation it is found that gland discharge *may* be elicited when even the sole of the foot is irritated, or almost any other region (with difficulty in the case of the tentacles), a greater intensity of stimulus is necessary than when applied on the back of the animal. Mechanical stimulation is in general more effective than chemical. Of the chemical excitants tried, only NaCl, LiCl, methyl and ethyl alcohols were successful, whereas such substances as pure amyl alcohol, numerous acids, alkalies and salts, in concentrations corresponding to those used in the case of the successful stimulating agents, as well as a series of alkaloids, were without effect when small volumes (a half or one c.c.) were applied to the mantle.

The designation of the mantle glands as repugnatorial is justified by observations in nature. Isopods (*Ligia*) and grapsoid crabs (*Sesarma,* and in some places, *Pachygrapsus*) abound in certain spots where the Onchidia take their airing. By prolonged watching, unequivocal instances have been noted in which these arthropods have come into direct contact with Onchidia, and in every case the glandular discharge took place, followed immediately by the retreat of the crab or isopod; it is not implied that the crabs were endeavoring to eat the snails, but it seemed rather that it was important for *Onchidium* to avoid being accidentally pushed off the rock into the water; it does not adhere to the rock with any great firmness, particularly under water, is easily dislodged, and if purposely pushed over the edge of the stone on which it may be creeping into the water, the animal finds it difficult if not impossible to return to its own nest.

Tests upon a number of animals (*e. g., Fundulus* from the land-locked brackish ponds at Bermuda) which could not by any possibility have ever come into contact with the *Onchidium* secretion, have invariably demonstrated the powerfully repugnant character of gland contents.

Finally, it is important to note that *Onchidia of whatever degree of pigmentation possess these repugnatorial glands, and in an equivalent state of development.* The behavior of the differently pigmented individuals, with reference to the use of the glands, is identical throughout the whole series.

V. Without entering upon a lengthy setting-forth of the several alternative possibilities which might readily be suggested in partial explanation of the foregoing series of facts, we may state our belief that an attempt at such explanation in terms of color-adaptation is confronted by serious, and indeed fatal, obstacles. From such a standpoint we are required to consider only the period during which the *Onchidium* is emerging from its nest and creeping about in the open. In the case of a dark *Onchidium* it is quite true that the animal is often very easily overlooked while in process of creeping over the *Modiolus* at the entrance of its nest; the color-match of the snail and the mussel is a fairly exact one. But an *Onchidium* does not resemble *Modiolus,* although of about the same size, when creeping upon algæ at the rate of 5 cm. per minute or faster. The paler kinds of *Onchidium* are, in almost every instance noted, a very precise match for their background, and sometimes careful search is necessary in order to detect them.

The non-homochromic pigmentation of the dark Onchidia would, in view of the presence and behavior of the poison glands, be of special interest in connection with the idea of warning coloration. But this view is rendered unintelligible in the face of the paler, concealingly-colored types. Moreover, the Bermudian Oncidiellas to which we have already alluded are very inconspicuous indeed, and they also possess poison-glands; their mode of life is quite different from that of *Onchidium,* since, although likewise inhabiting the intertidal zone, they retreat during low water to tiny holes,—dead serpula tubes and the like,—coming forth again only when covered by the water. These Oncidiellas are small, not more than 3 mm. long, and both light and dark individuals are in the highest degree difficult to detect when on their natural background; a delicate mottling of brownish pigment, in various shades, has a pronounced concealing effect in these places. Perhaps this accounts for the fact that *Oncidiella* has not previously been reported from the Bermuda area.

Not only does the idea of "warning" coloration become untenable for *Onchidium,* but the idea of adaptive concealing pigmentation is likewise without adequate support. The dark Onchidia are not concealingly colored, except during the transitory interval of their actual emergence from the nest, and even there they are easily seen, if looked for. The slime-coating, which would undoubtedly be of assistance in making them look like the background (for the silt it contains is formed on rocks where the pale bleached yellow algæ grow, and in other places where *Onchidium* lives), is almost invariably removed before the snail begins its promenade in the open. The relatively meager proportion of the Onchidia found pigmented in a truly homochromic manner is not explained by the idea of adaptive coloration, although the variation in the hues of differently tinted individuals would seem to provide favorable ground for the operation of selection. In this connection it might be suggested that *Onchidium floridanum* represents a comparatively recent addition to the fauna of Bermuda, and that the dark pigmentation common to this species and its immediate relatives throughout the world is even now in process of modification; but the fact that in the neighboring genus *Oncidiella* two more or less distinct general modes may be of widespread occurrence forbids the placing of any special emphasis upon this possibility, and even then, if correct, it would have no final significance for the conception of selective color-modification. If nutritive conditions, and temperature or light, or all three, do operate in a manner favorable to Onchidia of one or the other type in different places, the habit of living together in colonies might lead to a measurable degree of inbreeding, tending to prevent the general distribution of one variety of pigmentation, but at the same time a paler coloration, probably recessive in genetic behavior, would to that extent achieve a greater opportunity for perpetuation.

SUMMARY

VI. *Onchidium floridanum* Dall exhibits at Bermuda two chief types of pigmentation, a pale type tending to dull olive yellow, which tends to be concealingly colored, and a much more abundant type of dark blue-black appearance.

No correlation can be established between the pigmentation of an *Onchidium*—which there is some reason to consider the result of genetic factors primarily—and the hue of the substratum over which the snail creeps in the open at low tide.

O. floridanum possesses repugnatorial mantle-glands of an effective type, secreting a granular emulsion of substances having a strongly acid reaction and producing on moist surfaces of the human mouth a pronounced stinging sensation. Touch and pressure stimuli on the dorsal surface of the mantle are characteristically involved in releasing the discharge of these glands, which shoot their contents, in the form of a fine spray, to a distance about ten times the length of the *Onchidium* and with conspicuous accuracy of direction toward the source of excitation.

These facts are incompatible with the view that the coloration of *Onchidium* is determined or controlled by selection in the direction of homochromicity or concealment. Nor can they be understood in terms of ''warning'' coloration.

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